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Temperature Requirements of Some Percids and Adaptations to the Seasonal Temperature Cycle

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16. ABSTRACT Temperature requirements are reviewed for three North American percids (walleye, Stizostedion vitreum vitreum; sauger, S. canadense; and yellow perch, Perca flavescens), three Eurasian percids (perch, P. fluviatilis; pikeperch, S. lucioperca; and ruffe, Gymnocephalus cernua), and nine cohabitant fish species for comparison. Whole-organism responses are described for each species--primarily concerning reproduction, growth, survival, and activity. The percids are classified as temperature mesotherms and they are arranged in order of their thermal requirements as follows: pikeperch perches and ruffe sauger walleye. Perca and Stizostedion spp. are annual spawners with synchronous oocyte growth during fall through winter, culminating in spring spawning. Maturation occurs below 12°C. Spawning occurs from late February through early July at 2-26°C over their geographic ranges. Oocyte growth of ruffe is asynchronous, accelerated by warm temperatures; batch spawning occurs over a prolonged period, from mid-April through July at 11-18°C. Physiological optima range from 22°C for sauger and walleye to 25°C for perch and 27°C for pikeperch. The ultimate upper incipient lethal temperatures of percids range from 29 to 35°C, depending on species and experimental conditions.

Percid life phases are uniquely adapted to the seasonal temperature cycle of a temperate climate. Mechanisms of adaptation to the seasonal temperature cycle are discussed. No uniform mechanism of population regulation or resiliency is apparent for different acclimatization conditions. Therefore, management regulations for a given species should not be universally applied throughout its geographic range.

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Temperature Requirements of Some Percids and Adaptations to the Seasonal Temperature Cycle[1]

KENNETH E. F. HOKANSON

U.S. Environmental Protection Agency, Monticello Ecological Research Station, Environmental Research Laboratory-Duluth, Monticello, Minn. 55362, USA

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Temperature requirements are reviewed for three North American percids (walleye, *Stizostedion vitreum vitreum*; sauger, *S. canadense*; and yellow perch, *Perca flavescens*), three Eurasian percids (perch, *P. fluviatilis*; pikeperch, *S. lucioperca*; and ruffe, *Gymnocephalus cernua*), and nine cohabitant fish species for comparison. Whole-organism responses are described for each species — primarily concerning reproduction, growth, survival, and activity. The percids are classified as temperature mesotherms and they are arranged in order of their thermal requirements as follows: pikeperch > perches and ruffe > sauger > walleye. *Perca* and *Stizostedion* spp. are annual spawners with synchronous oocyte growth during fall through winter, culminating in spring spawning. Maturation occurs below 12°C. Spawning occurs from late February through early July at 2–26°C over their geographic ranges. Oocyte growth of ruffe is asynchronous, accelerated by warm temperatures; batch spawning occurs over a prolonged period, from mid-April through July at 11–18°C. Physiological optima range from 22°C for sauger and walleye to 25°C for perch and 27°C for pikeperch. The ultimate upper incipient lethal temperatures of percids range from 29 to 35°C, depending on species and experimental conditions.

Percid life phases are uniquely adapted to the seasonal temperature cycle of a temperate climate. The maturation limit (10°C) for *Perca* spp. approaches the minimum winter temperature in lowermost latitudes of their distribution. Increasing temperature requirements of successive early life phases show how percids adapt to the spring spawning period. Spawning begins in a temperature range that optimizes gamete viability. Temperature has little effect on duration of the phases of gonad maturity in *Perca* and *Stizostedion* spp. These fishes adapt to different temperature regimens by shifting spawning temperatures, while spawning time changes only slightly, sometimes at the expense of gamete viability. Greater differences in spawning time observed at geographical extremities of their range are believed to be due to longer term adaptations that determine time of first maturity rather than adaptations of the adult maturation cycle. Ruffe are more adaptable, spawning several batches of ova under favorable environmental conditions. Summer distributions of *Perca* spp. lie between the 16 and 31°C isotherms. These values represent the lower limit to normal maturation of adults and growth of young and the upper temperature for zero net biomass gain, respectively. Only maximal temperatures in lower latitudes approach the ultimate upper incipient lethal temperature of a species. Fish adapt to different thermal characteristics by changes in their avoidance/preference response, diel activity cycles, and seasonal migrations. No uniform mechanism of population regulation or resiliency is apparent for different acclimatization conditions. Therefore, management regulations for a given species should not be universally applied throughout its geographic range.

Key words: Percidae, temperature requirements, adaptations, seasonal temperature cycles, *Perca*, *Stizostedion*, *Gymnocephalus*, temperature classification, literature synthesis

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Nous passons en revue les exigences thermiques de trois percidés nord-américains (le doré jaune, *Stizostedion vitreum vitreum*; le doré noir, *S. canadense*; et la perchaude, *Perca flavescens*), trois percidés eurasiens (la perche, *P. fluviatilis*; le sandre, *S. lucioperca*; et la perche goujonnière, *Gymnocephalus cernua*), que nous comparons avec celles de neuf espèces de poissons habitant les mêmes milieux. Nous décrivons pour chaque espèce les réponses de

[1]This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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l'organisme entier — principalement celles touchant la reproduction, la croissance, la survie et l'activité. Nous classifions les percidés comme mésothermes tempérés et les disposons par ordre d'exigences thermiques comme suit: sandre > perches et perches goujonnières > doré noir > doré jaune. *Perca* et *Stizostedion* spp. fraient annuellement, avec croissance synchrone des ovocytes en automne et durant tout l'hiver, culminant avec la ponte au printemps. La maturation se produit à une température inférieure à 12°C. La fraie a lieu depuis la fin de février jusqu'au début de juillet à 2–26°C dans l'aire de toutes les espèces. La croissance des ovocytes de la perche goujonnière est asynchrone, étant accélérée par de chaudes températures; la fraie par lots se produit sur une longue période, de la mi-avril à juillet inclusivement à 11–18°C. Les optimums physiologiques vont de 22°C pour le doré noir et le doré jaune à 25°C pour la perche et 27°C pour le sandre. Les températures supérieures ultimes du début des mortalités des percidés varient de 29 à 35°C, selon l'espèce et les conditions expérimentales. Les phases de la vie des percidés sont adaptées de façon unique au cycle de températures saisonnières d'un climat tempéré. La limite de maturation (10°C) de *Perca* spp. se rapproche du minimum de température d'hiver aux plus basses latitudes de leur distribution. Les exigences thermiques croissantes des phases successives du début de la vie montrent comment les percidés s'adaptent à la période printannière de fraie. La fraie commence à une gamme de températures qui donne une viabilité optimale des gamètes. La température a peu d'effet sur la durée des phases de maturation des gonades chez *Perca* et *Stizostedion* spp. Ces poissons s'adaptent à différents régimes de température en déplaçant les températures de fraie, alors que la période de fraie ne change que légèrement, parfois au dépens de la viabilité des gamètes. On croit que les plus grandes différences dans la période de fraie observées aux extrémités géographiques de leur aire sont dues à des adaptations à plus long terme qui déterminent l'époque de la première maturité, plutôt qu'à des adaptations du cycle de maturation adulte. La perche goujonnière est plus adaptable, pondant plusieurs lots d'œufs quand les conditions ambiantes sont favorables. La distribution estivale de *Perca* spp. se situe entre les isothermes de 16 et 31°C. Ces valeurs représentent la limite inférieure d'une maturation normale des adultes et d'une croissance des jeunes, et la température supérieure pour un gain nul de biomasse nette, respectivement. Seules les températures maximales aux basses latitudes se rapprochent de la température supérieure ultime du début des mortalités d'une espèce. Les poissons s'adaptent à différentes caractéristiques thermiques en changeant leur réponse d'évitement/préférence, leur cycle nycthéméral d'activité et leurs migrations saisonnières. Il ne semble pas y avoir de mécanisme uniforme de réglage ou de résistance des populations sous différentes conditions d'acclimatation. Les règlements concernant la gestion d'une espèce donnée ne devraient donc pas être universellement appliqués dans toute son aire géographique.

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THE purpose of this review is to describe the temperature requirements and adaptations to the seasonal temperature cycle of some commercially important freshwater percids: the walleye (*Stizostedion vitreum vitreum*), sauger (*Stizostedion canadense*), and yellow perch (*Perca flavescens*) of North America and the perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*), and ruffe (*Gymnocephalus cernua*) of Eurasia. The temperature requirements of nine cohabitant species are described for comparison so that a temperature classification scheme could be developed for percids and other freshwater fishes. The present range of self-sustaining populations of these percids extends from about 30 to 75° N lat. (Weatherley 1963a; Deedler and Willemsen 1964; Berg 1965; Scott and Crossman 1973). The species are adapted to temperate climates of the northern hemisphere, although perch were successfully introduced into Australia. Water temperatures in percid habitat vary seasonally from <4°C for more than 8 mo in the northernmost latitudes to about 32°C in the southernmost extremities of the percid range.

As PERCIS evolved from management's needs for information on exploitation, habitat modification, and rehabilitation of percid communities, this paper is limited to whole-organism responses — specifically reproduction, growth, survival, and activity. These responses encompass the effects of temperature on the physiology of fishes, are most readily measured in field-stock assessment, and are important parameters in population-dynamics models of yield and production which can be used to evaluate man-imposed stresses.

The temperature requirements of these percids are described for each response. Seasonal changes in thermal responsiveness of percids are of special interest because they modify the effects of temperature on different phases of the life cycle, maturation cycles, spawning times, migrations, activity, and ultimately distribution and abundance of the species. I describe effects of temperature on percids from several unpublished

TABLE 1. Temperature classification of temperate-climate[a] freshwater fish.

Classification	Criteria	Species
Temperate stenotherm	Gonadal growth phase in summer, <20°C Spawning in fall to spring, <15°C Physiological optimum, <20°C Ultimate upper incipient lethal temp, <26°C	Brook trout (*Salvelinus fontinalis*) Rainbow trout (*Salmo gairdneri*) Lake herring (*Coregonus artedii*)
Temperate mesotherm	Gonadal growth phase in fall and winter, <12°C Spawning in spring, 3–23°C Physiological optimum, 20–28°C Ultimate upper incipient lethal temp, 28–34°C	White sucker (*Catostomus commersoni*) Northern pike (*Esox lucius*) Percids reviewed herein
Temperate eurytherm	Gonadal growth phase during long days, >12°C Spawning in spring to fall, 15–32°C Physiological optimum, >28°C Ultimate upper incipient lethal temp, >34°C	Largemouth bass (*Micropterus salmoides*) Bluegill (*Lepomis macrochirus*) Tench (*Tinca tinca*) Carp (*Cyprinus carpio*)

[a]The use of the term *temperate* as a prefix in classification represents the ability of most temperate-climate species to survive temperatures near freezing (<4°C). Therefore, description of a species' thermal requirements reflects their relative biokinetic range of tolerance, performance, and activity.

papers within my organization to establish percid requirements, since key information on reproduction and activity is lacking. Graphical endpoints from experimental data are defined so that temperature relationships among percids and cohabitant species can be compared. Standardized methods were not used. Therefore, I describe the effects of experimental factors to explain variation in temperature responses and to facilitate comparisons among species. Natural-history observations supplement experimental data where appropriate. Species of *Perca* have been studied most often; comparable data are rather sparse for other percids, particularly Eurasian species. Therefore, temperature requirements of *Perca flavescens* and *P. fluviatilis* are compared with temperature limits of distribution to establish the physiological and ecological significance of graphical endpoints used herein. These comparisons suggest several adaptive mechanisms to the seasonal temperature cycle. Based on autecology relationships, I suggest a hypothesis concerning percid population adaptations to different temperature regimens that may have useful management implications.

Temperature Classification

Percids can be classified as temperate mesotherm, which reflects the intermediate temperature niche of percids in fish communities. A classification scheme is needed that recognizes the species with intermediate requirements, especially among the warmwater species. The use of the term *temperate* as a prefix in classification represents the ability of most temperate-climate species to survive temperatures near freezing (<4°C). Therefore, description of a species' thermal requirements reflects their relative biokinetic range of tolerance, performance, and activity. A temperature classification scheme that recognizes three limits of thermal requirements and modes of reproduction is proposed for temperate-climate species (Table 1). Temperate stenotherms include *Salvelinus fontinalis*, *Salmo gairdneri*, and *Coregonus artedii*; other temperate mesotherms include *Catostomus commersoni* and *Esox lucius*, which are commonly associated with percids; and temperate eurytherms include *Micropterus salmoides*, *Lepomis macrochirus*, *Tinca tinca*, and *Cyprinus carpio*. Further classification is not warranted until the temperature requirements of various species and life phases are accurately described on the basis of uniform criteria and procedures.

Percids may be associated with warm- and cold-

water species. In cold-water lakes percids occupy the surface waters and embayments, whereas cold-water Salmonidae occupy the deeper offshore areas (Hile and Juday 1941; Echo 1955; McCormack 1965; Ryder 1968; Thorpe 1974). Percids are known to feed on cold- and warmwater species. Percids were confined to deeper water in summer in southernmost latitudes, and species adapted to warmer water were in the surface waters (Dendy 1948). Depth distribution in these waters can be limited by warm surface waters and low dissolved oxygen concentrations in the hypolimnion. Percids are generally among the less abundant species around thermal plumes in all seasons of the year (Alabaster and Downing 1966; EIFAC 1968; Boytsov 1971; Gammon 1971; Horoszewicz 1973; Neill and Magnuson 1974).

Percids can be arranged in the following order of thermal requirements: pikeperch > perches and ruffe > sauger > walleye. Pikeperch clearly have higher thermal requirements for all responses than the perches. Sauger and walleye have distinctly lower physiological optima and lethal temperatures than the perches. Walleye require lower temperatures for spawning than the sauger, which is the principal difference between the two species. On the basis of available data, one cannot distinguish between the temperature requirements of Eurasian perch, yellow perch, and ruffe. Successful hybridization between ruffe and Eurasian perch also suggest similarities between the two species (Kammerer 1907). These subtle differences in thermal tolerance may be reflected in their geographical distribution.

Experimental conditions can be a greater source of variation than specific differences among percids. A difference in thermal response between two stocks does not imply genotypic variation (Fry 1957). No racial differences in thermal tolerance have been demonstrated for a wide variety of fishes from isolated habitats and different thermal regimens (Hart 1952; Brown and Feldmeth 1971; Horoszewicz 1973). Hubbs (1971) noted that walleye eggs from Lake Meredith, Texas (introduced from Iowa), developed at 20°C, whereas eggs from the Thames River, Ontario, had poor survival at 16.5°C. He suggested that there were racial differences in thermal tolerance. However, he did not account for differences in egg quality as influenced by fertilization temperature, which also contributes to the percentage of eggs that hatch. Lack of comparable experimental data does not imply that no racial differences exist. Other attributes besides temperature tolerance, such as light sensitivity, bioenergetics, maturation rate, swimbladder adaptations to depth, feeding, and migratory behavior, may separate a species along a habitat gradient.

Reproduction

Fish reproduction involves a complex sequence of events, including gonad growth and gamete maturation, spawning migration, release of viable gametes, embryo and larval development, and the beginning of independent feeding by larvae. Fishes of the temperate climate respond to regular seasonal cycles of temperature and day length. Such rhythms ensure maturation and spawning at regular times in each locality. The critical temperatures that permit successful maturation, spawning, and gamete viability are of special interest to this review.

Maturation cycle — *Perca* and *Stizostedion* spp. have synchronous oocyte growth and are annual spawners that lay all their eggs at one time in shallow water in the spring (Koshelev 1963; Breder and Rosen 1966). Turner (1919) described the seasonal cycle in the spermary of yellow perch from Lake Mendota, Wisconsin: the testis was smallest from late June to late August, which is a period of germ-cell migration, proliferation, and growth, and maximum water temperature. The volume of the testis began to increase in September and reached maximum size in early November. Spermatids and spermatozoa began to form in early September and remained in the mature stage until spawning in the spring. The increase in testicular volume and beginning of spermatogenesis were contemporaneous with the beginning of a seasonal decrease in water temperature. Testicular volume declined rapidly from March through June as spermatozoa were expelled during spawning in a period of rising water temperature. LeCren (1951) observed a similar testicular cycle in the Eurasian perch from Lake Windermere, England.

The principal growth phase of the ovaries of *Perca* and *Stizostedion* spp. takes place during the coolest seasons, when body growth ceases. Koshelev (1963) described the seasonal oogenesis cycle in Eurasian perch from Lake Glubokoe, USSR, and LeCren (1951) described the seasonal cycle in the ovary–body-weight ratio of perch from Lake Windermere, England, as follows: after the fish spawns, the ovaries pass into a transitional stage of maturity (stage VI–II), which generally lasts for a month, and is characterized by resorption of the remnants from the emptied follicles. The ovary–body-weight ratio declines from 3 to 1% of the body weight during this period. A period of no ova growth but active oogenesis (stage II) lasts from the middle of June through August. The active growth phase of the ova and development of numerous vacuoles (stage III) lasts 45–60 days, from early September to late October. The start of formation of fat and yolk in the oocytes (stage IV) begins in November. Synchronous growth of oogonia continues until spawning in May when the ovary averages 20% or more of the body weight. The total period of active ova growth and vitello-

genesis lasts about 220 days in perch. In contrast, ovulation and spawning (stage V) last for only a few days. Maturation cycles similar to Eurasian perch have been observed for yellow perch from Lake Michigan (Brazo 1973), walleye from Lake Ontario (Payne 1964), and pikeperch from the USSR (Golovanenko et al. 1970).

Resorption of oocytes or lengthening the post-spawning stage (VI–II) due to unfavorable conditions of the habitat can interfere with development of the next year's batch of oocytes in fish with synchronous oocyte growth (e.g. *Perca* and *Stizostedion* spp.). Deficiency in food and poor growth conditions in summer can reduce the rate of the resorptive processes and delay the period of oocyte growth sufficiently to cause them to miss the following spawning period (Eschmeyer and Smith 1943; Koshelev 1963; Forney 1965; Scott and Crossman 1973). Delayed or interrupted spawning seasons can lead to resorption of ova in walleye (Derback 1947; Schumann 1964) and pikeperch (Golovanenko et al. 1970). A large number of Eurasian perch failed to spawn after unusually severe winters in Windermere, England (LeCren 1965). Ova resorption interferes with development of the next batch of oocytes in pikeperch (Kukuradze 1968) and walleye (W. B. Horning II, U.S. EPA, Newton, Ohio, personal communication), which prevents reproduction in the following spawning period. Growth of the new batch of oocytes begins in these species only after completion of all the resorptive processes in the ovary (Koshelev 1963).

Ruffe are more adaptable to changing environmental conditions than *Perca* and *Stizostedion* spp. In ruffe, oocyte growth is asynchronous and spawning is intermittent (Koshelev 1963). Ruffe differ from the other percids in having a faster oocyte growth rate in the period of fat and yolk accumulation in spring and early summer and less oocyte growth over winter. The first batch of oocytes matures (stage III–V) in 165 days during winter and spring and the second in 30 days during summer. The faster oocyte growth rate during vitellogenesis leads to maturation of several batches of oocytes during the year and prolongs the spawning period where conditions are more favorable. Stage II is absent and oocytes are in various stages of development or resorption throughout the spawning period. Resorption of unspawned ova does not interfere with growth of the next batch of oocytes because ova growth and resorption occur simultaneously in this species (Koshelev 1963).

Maturation requirements — a winter minimum temperature of 10°C is near the upper limit for maturation of gonads in yellow perch and walleye. Jones et al. (1977) reared adult yellow perch from Minnesota in the laboratory under a natural day-length cycle and 16 thermal regimes from October through June. The maximum percentage of females spawning declined as the winter minimum temperature at which they had been held increased (Fig. 1). Optimal conditions for maturation that terminated in spawning occurred when fish were exposed to 6°C or lower for 185 days from October 30, whereas no viable spawning occurred when the fish were maintained at a minimum temperature of 12°C or higher. In preliminary studies, viable spawnings were observed among perch held at a minimum of 12°C except for 1½ mo at 8°C in winter. Chill durations <185 days from October 30 reduced spawning in these treatments. High temperatures at the end of these treatments may have blocked maturation or spawning. Miller (1967) reported that introduced walleye failed to reproduce in California reservoirs. These waters became essentially isothermal in winter at temperatures ranging from 10 to 12.5°C (G. W. McCammon, Department of Fish and Game, Sacramento, Calif., personal communication). Higher temperatures are apparently required for maturation of their oocytes in summer (Koshelev 1963).

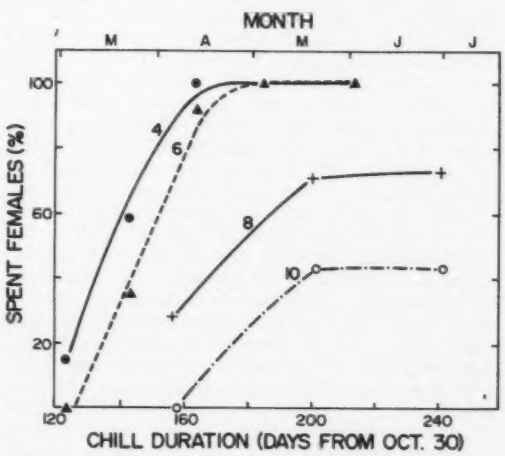

FIG. 1. Percentages of female yellow perch (*Perca flavescens*) that spawned during exposure to four chill temperatures (4, 6, 8, and 10°C) of different durations (123–242 days from October 30). Temperature was increased at a rate of 2°C/wk to a maximum of 20°C after termination of the exposure to the various chill temperatures (from Jones et al., Environmental Research Laboratory–Duluth, unpublished data).

Time of spawning — Percids spawn during periods of rising temperature in the spring. The rapid adjustment of introduced species to new temperature regimes suggests that spawning time is strongly influenced by local environmental factors and that each stock has a different reproductive cycle. Seasonal changes in day-length and temperature cycles set finite limits on the length of the spawning season for a given fish stock by influencing maturation and ova viability (Hokanson and Biesinger 1977). Upon completion of maturation, spawning is triggered by heterogenous stimuli, such as a rising water temperature, suitable spawning substrate, and courtship behavior (Deelder and Willemsen 1964). Yellow perch exposed to various thermal treatments, previously described, spawned from April 12 to June 20 (Jones et al., Environmental Research Laboratory-Duluth, unpublished data). Of all viable spawnings, 80% occurred during the normal spawning season of this stock, from May 10 to June 8. Yellow perch exposed to warmer thermal regimes spawned only slightly earlier and at somewhat higher temperatures than those exposed to colder temperatures (Fig. 2). For chill durations longer than 214 days, spawning began before termination of the chill period at low constant temperatures; rising temperatures were not required to trigger spawning. Thus, spawning temperature appears to be a function of the prevailing water temperature at the time each stock completes maturation and ovulation.

Percids show a greater difference in spawning time at geographical extremities of their range than for any given stock. Although *Perca* and *Stizostedion* spp. may spawn for only 1–3 wk in any given locality, they spawn from late February to early July in different localities (Table 2). Spawning of Eurasian perch in lower latitudes occurs earlier in the year at higher temperatures than in higher latitudes (Thorpe 1977). In reproducing populations of Eurasian perch that have been established in the southern hemisphere, the fish spawn from late August to October during the rising temperature period (Lake 1959). The importance of the temperature regimen in timing of spawning was further emphasized in Turkey, where pikeperch were introduced into two lakes with different temperature regimes. Spawning occurred in late February and March in the lake with the higher temperature, and as late as May–June in the colder lake (Aksiray 1961). Ruffe spawn one to three batches of ova over a 2-mo spawning season in Lake Glubokoe, USSR (Koshelev 1963); they spawn from mid-April through July over their geographic range (Table 2).

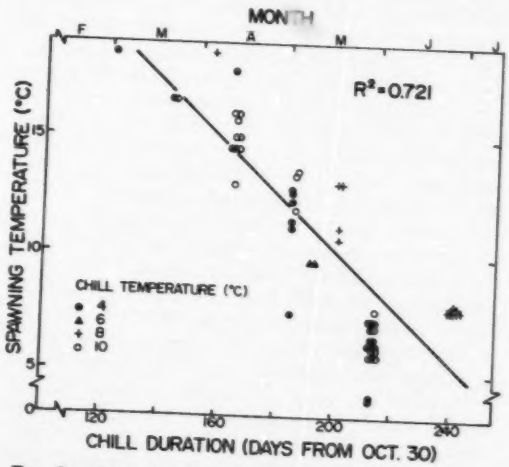

FIG. 2. Spawning temperature observed at the time of laboratory spawning of yellow perch from Minnesota that had been exposed to four chill temperatures for various periods (from Jones et al. Environmental Research Laboratory–Duluth, unpublished data). Chill duration was the time of exposure to chill temperatures from October 30 to beginning of spring rise in temperature at 2°C/wk.

Spawning temperature and gamete viability — Percids spawn at temperatures that enhance gamete viability. Smith and Koenst (1975) acclimated mature walleyes to six temperatures from 6 to 21°C. After the fish became ripe, they were stripped and the eggs were fertilized at their respective acclimation temperatures. The eggs fertilized at each acclimation temperature were incubated at each of six incubation temperatures from 6 to 21°C to separate the effects of acclimation (parental) temperature and incubation (embryo) temperature on the hatchability of eggs. The effect of incubation temperature on hatchability was modified substantially by acclimation (parental) temperature (Fig. 3). The principal effect of acclimation temperature was on gamete viability, which was highest at 6–9°C, the temperature range most frequently observed on the spawning grounds. Independent of the effect of fertilization temperature, the highest percentage hatch was at incubation temperatures of 9–15°C.

Yellow perch held at various treatments produced viable ova at temperatures from 3.9 to 18.6°C (Jones et al., Environmental Research Laboratory-Duluth, unpublished data). Eighty percent of all viable spawnings were produced at temperatures from 6.2 to 16.0°C. Gamete viability was highest at 8–11°C.

TABLE 2. Relationships between median temperature tolerance limits of embryos and water temperatures observed on spawning grounds of various percids.

Species	Embryo TL50 (°C)[a]		Spawning temp (°C)[b]		Spawning date[b]	
	Lower	Upper	Lowest	Highest	Earliest	Latest
Walleye (*S. v. vitreum*)	<6.0	19.2[d]	2.2 (Wis.)[j]	15.6 (Wis.)[j]	Mar. 10 (Okla.)[r]	Late June (Can)[v]
Sauger (*S. canadense*)	6.0	>20.9[d]	4 (N. Dak.)[j]	14.4 (Tenn.)[p]	Mid-Mar. (Ala.)[s]	June 25 (N. Dak.)
Yellow perch (*P. flavescens*)	6.8	19.9[e]	2.0 (Md.)[k] 3.9 (Minn.-Lab)[l]	18.6 (Minn.-Lab)[l]	Late Feb. (Md.)[k]	Early July[w] (Lake Mich.)
Eurasian perch (*P. fluviatilis*)	6.1	20.2[f]	5 (USSR)[m]	18.0 (Pol.)[n] 19.0 (Czech.)[n]	Late Feb. Late Aug. (Aust.)[t]	July (USSR)[x]
Ruffe[c] (*G. cernua*)			11.6 (Czech.)[n]	18 (Neth.)[aa]	Apr. 17 (Austria)[n]	Late July (USSR)[y]
Pikeperch (*S. lucioperca*)	10.0 9.0	21.5[g] 24.0[h]	4.5 (USSR)[o]	26 (Finl.)[o]	Late Feb. (Turk.)[h]	Early July (USSR)[z]

[a]Median tolerance limits based on normal hatch of eggs incubated at constant temperature from fertilization to hatch.
[b]Location indicated in parentheses.
[c]Available references limited; therefore, data are common values observed rather than extremes.
[d]Smith and Koenst (1975); [e]Hokanson and Kleiner (1974); [f]Swift (1965); [g]Muntyan (1967); [h]Deelder and Willemsen (1964); [i]Priegel (1970); [j]Carufel (1963); [k]Muncy (1962); [l]Jones et al. (Environmental Research Laboratory-Duluth, unpublished data); [m]Kovalev (1973); [n]Bastl (1969); [o]Zhdanova (1966); [p]Gordon Hall, TVA, Norris, Tenn., personal communication; [q]EIFAC (1968); [r]Grinstead (1971); [s]Wrenn (1974); [t]Weatherley (1963a); [u]Kammerer (1907); [v]Scott and Crossman (1973); [w]Brazo (1973); [x]Berg (1965); [y]Koshelev (1963); [z]Rizvanov (1970); [aa]Willemsen (1977).

Both species of perch spawn at temperatures from 4 to 19°C throughout their geographic ranges (Table 2). Walleye (2.2–15.6°C) and sauger (4–14.4°C) have the lowest spawning temperatures and pikeperch (4.5–26°C) has the highest. Spawning data for ruffe are rather sparse and represent only common values observed on the spawning grounds. In Lake Ilmen, USSR, ruffe and perch usually spawn at about the same time, before pikeperch (Kovalev 1973).

Favorable spawning temperatures may enhance gamete viability through production of specific gonadotropins, which completes maturation and induces ovulation. In contrast to the long growth phase of maturation in *Perca* and *Stizostedion* spp., ovulation or initiation of resorption takes place within 1–3 days, depending on conditions prevailing on the spawning grounds (Koshelev 1963; Golovanenko et al. 1970). Mature females that migrate towards the spawning grounds at temperatures near their lower spawning threshold do not yield viable ova initially, but become fully ripe later in the migration or on the spawning grounds (Deelder and Willemsen 1964; Priegel 1970; Johnson 1971). During the final 2 wk of the maturation cycle of pikeperch, the quantity of protein in the ovary increased 89%, blood hemoglobin decreased 20%, serum protein decreased 21%, protein content of the liver decreased 19%, and lipid content of the liver decreased 34% (Golovanenko et al. 1970). This period coincided with the rise of temperature to the optimum spawning temperature during the migration. Use of gonadotropin injections on female pikeperch at this time is known to hasten the terminal stages of maturation and induce ovulation of matured oocytes (Putina et al. 1970). Balandin (1941) reported that pikeperch that were given a pituitary injection and then released into ponds spawned at 5–8°C, which was below the temperature at which they normally reproduced. The induced ripening of fish at temperatures below the critical ones by means of injection of gonadotropin is a strong indication that a deficiency of gonadotropin is responsible for the cessation of gametogenesis at low temperatures (Atz 1957), and possibly at higher temperatures as well.

Embryonic and larval requirements — Successive early life phases of *Perca* and *Stizostedion* have temperature requirements that increase with morphological differentiation. The temperature requirements of yellow perch are illustrated in Fig. 4. The median tolerance limits (TL50) of successive embryonic and larval phases of yellow perch reported by Hokanson and Kleiner (1974) were 3.7–21°C in early embryonic stages (fertilization to neural keel) and 7.0–22.9°C in later embryonic stages (neural keel to hatching). The lower TL50 for production of swim-up larvae was 9.8°C. Newly hatched yellow perch larvae tolerated a temperature range of 3–28°C for 24 h when incubated and hatched at 18°C (Environmental Research Laboratory-Duluth, unpublished data); however, larvae were inactive at 5.3°C. Optimum yields of swim-up larvae were produced when initiated incubation temperatures (4.9–10.0°C) were increased 1 deg. C/day (range 4.9–24.3°C). Rising temperature regimes also favored shorter hatching periods and lower incidence of abnormalities than did constant temperatures. In pikeperch, rising temperature regimes favored shorter hatching periods and lower incidence of abnormalities (Muntyan 1975) than did constant incubation temperatures (Muntyan 1967). Optimum temperatures for development of pikeperch increased from 12 to 20°C for spawning, 14 to 23°C for larvae (1–7 days old),

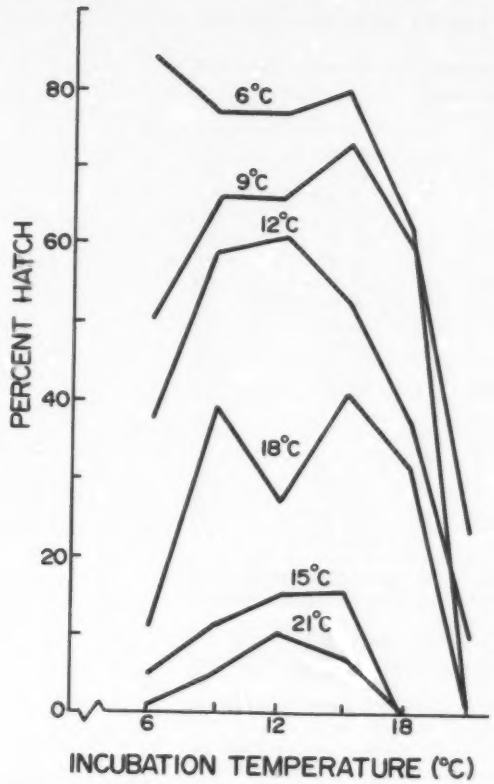

FIG. 3. Percentage of walleye (*Stizostedion vitreum vitreum*) eggs that hatched at various incubation temperatures after fertilization at six temperatures from 6 to 21°C (from Smith and Koenst 1975).

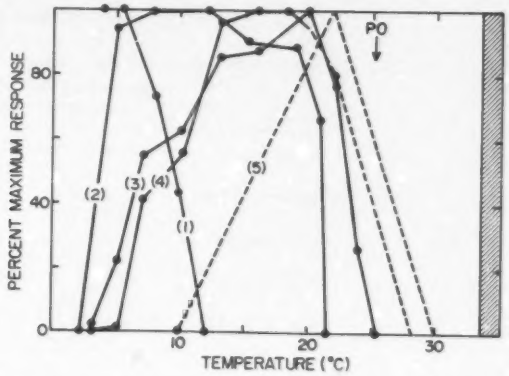

FIG. 4. Temperature limits for survival of different stages in the life cycle of yellow perch expressed as percentages of maximal responses. (1) Maximal percentages of females spawning after exposure to various chill temperatures. (2) Egg survival from fertilization to formation of the neural keel (C. F. Kleiner, U.S. EPA, Monticello, Minn., personal communication). (3) Egg survival from neural keel formation to hatch. (4) Larval survival from hatch to swim-up stage. (5) Predicted survival of feeding larvae on excess rations based on larval rearing observations. Arrow designates physiological optimum (PO) of juveniles and shaded area the zone of thermal resistance, where survival is time-dependent, bounded on the left by the ultimate upper incipient lethal temperature, for juveniles.

and 14 to 26°C for larvae (22–35 days old) (Zhdanova 1966). The upper lethal temperature for larvae (4.5–5.8 mm long) was 30–32°C, and the lower lethal limit was 6.0–6.5°C. A drop in water temperature below 10°C was not considered desirable for larvae (Woynarovich 1963; Zhdanova 1966). Temperature fluctuations within normal tolerance limits of walleye embryos were not considered harmful (Allbaugh and Manz 1964).

The range of observed spawning temperatures in the percids reviewed corresponds closely with embryo tolerance limits (Table 2): the TL50 limits are lowest in the walleye (<6.0–19.2°C), highest in pikeperch (9–24°C), and intermediate in sauger and the two perches (6.0–21°C). Similar trends were also observed for extreme spawning temperatures. Where field observations were most extensive, as in perch, the maximum spawning temperature corresponded closely to the upper TL50 for embryos. The lowest spawning temperature observed for each species, however, was 2–4 deg C lower than the lower TL50 limit for embryos. A closer correspondence may exist between the lowest spawning temperature and temperature tolerance of early embryonic phases, as for yellow perch (3.7°C). In contrast, temperate stenotherms are adapted to temperatures below 15°C for spawning and embryo development; and temperate eurytherms to temperatures between 15 and 32°C (Table 3).

Temperatures required to initiate feeding among percid larvae appear to be higher than those required by embryos. No perch and ruffe larvae survived Kammerer's (1907) feeding trials at 10°C; however, he had some survive at higher temperatures. Hubbs (1971) observed that three of seven samples of larval yellow perch fed at 12.5°C, as did one of nine samples at 9.5°C. Smith and Koenst (1975), who reared larval sauger and walleye to 40 mm, reported that, for each species, only 1% survived at 18°C and 8% at 21°C; none survived at 15°C or less. Similar results were observed by Olson (1974). Hale and Carlson (1972), who reared yellow perch larvae at 20–21°C, obtained a mean survival of 63%

TABLE 3. Temperature requirements of some fish species associated with percids.

Species	Reproduction range (C)[a]	Physiological optimum (C)[b]		Lethal temp (°C)[c]	
Brook trout	1.6–12.7[d,e]	15.6[f]	(L)	20.1[g]	(L)
	0.3–10[f]	16.1[e]	(A)	25.3[g]	(J)
Rainbow trout	3–15[g]	17.2[f]	(J)	25.0–26.5[f,aa,bb]	(J)
	0.3–15[f]			21[cc]	(A)
Lake herring	1.2–9.1[h]	18.1[e]	(L)	19.8[e]	(L)
	1.1–5.0[i]			26.2[dd]	(J)
White sucker	8.1–21.2[j]	26.9[j]	(L)	30.5[j]	(L)
	6.1–23.3[k]			29.3–31.2[ee,ff]	(J)
Northern pike	6.9–19.2[l]	26[l]	(L)	28.4[l]	(L)
	3–18.5[l]			33[gg]	(J)
				29.0[hh]	(A)
Largemouth bass	11.6–27.9[m]	30.0[r]	(L)	36.4[ii]	(J)
	15.6–26.7[f]				
Bluegill	21.9–33.8[n]	30.1[w]	(J)	37.3[n]	(J)
	17.2–32.3[f]	32.3[x]	(J)		
Trench	16.5–32.2[o]			33.8[jj]	(J)
	14–27.5[o]			39.3[kk]	(J)
Carp	12.5–30.0[p]	32.0[y]	(J)	35.7[ll]	(J)
	16–26[q,r]			40.9[kk]	(J)

[a]Spawning temperature range observed in the field (upper value); lower and upper TL50s of eggs incubated at constant temperatures from fertilization to hatch in the laboratory (lower value).

[b]Physiological optimum based on growth data. Higher value for bluegill and value for carp are final preferenda in laboratory. L, larvae; J, juvenile; or A, adults.

[c]Ultimate upper incipient lethal temperature. Higher values for tench and carp are critical thermal maxima. L, larvae; J, juvenile; or A, adults.

[d]Embody (1934); [e]Hokanson et al. (1973b); [f]Hokanson and Biesinger (1977); [g]Kwain (1975); [h]Colby and Brooke (1970); [i]Carlander (1969); [j]McCormick et al. (1977); [k]Trautman (1957); [l]Hokanson et al. (1973a); [m]Kelly (1968); [n]Banner and Van Arman (1973); [o]Reznichenko et al. (1968); [p]Keiz (1959); [q]Swee and McCrimmon (1966); [r]Sigler (1958); [s]McCormick et al. (1972); [t]Hokanson et al. (1977); [u]McCormick et al. (1971); [v]Strawn (1961); [w]Lemke (1977); [x]Ferguson (1958); [y]Pitt et al. (1956); [z]Fry et al. (1946); [aa]Alabaster and Welcomme (1962); [bb]Bidgood and Berst (1969); [cc]Coutant (1970); [dd]Edsall and Colby (1970); [ee]Brett (1944); [ff]Hart (1947); [gg]Scott (1964); [hh]W. B. Horning II, U.S.EPA, Newton, Ohio, personal communication; [ii]Hart (1952); [jj]Alabaster and Downing (1966); [kk]Horoszewicz (1973); [ll]Black (1953).

after 3 wk. Kudrinskaya (1970b) determined that ration size had a pronounced effect on growth and survival of perch and pikeperch larvae at 19.3°C, but had less effect at 16.0°C. These observations suggest that feeding and survival of well-fed percid larvae is possible above 10°C and optimal above 20°C. Temperature optima for survival would be lower if rations were restricted. The temperature requirement of yellow perch larvae deduced from these feeding trials is illustrated in Fig. 4.

Studies on the effects of temperature and ration size over the biokinetic range of percid larvae are needed for a fundamental understanding of the critical period of survival. Temperature requirements of feeding percid larvae are poorly known; high mortality of larvae occur when sufficient quantities of preferred food organisms are lacking (Menshutkin et al. 1968; Kudrinskaya 1970a; Hale and Carlson 1972). Larval percids have similar specific food requirements at the start of feeding — principally copepod nauplii, the large rotifer *Polyarthra*, and small cladocerans, such as *Bosmina* and *Chydorus* (Woynarovich 1960; Deelder and Willemsen 1964; Menshutkin et al. 1968; Siefert 1972). Many factors other than temperature and food density tend to reduce survival of percid larvae — such as high light

intensity, high larval density (resulting in cannibalism), and transfer methods between aquaria (Woynarovich 1960; Hale and Carlson 1972; Olson 1974).

Embryonic and larval development rate — The median times required for percids to reach various stages of embryonic and larval development decrease exponentially with increasing temperature. Hokanson and Kleiner (1974) described the median times required to reach various morphological stages and physiological events in yellow perch embryos and larvae at various constant temperatures (Fig. 5). Median time to hatch ranged from 6 days at 19.7°C to 51 days at 5.4°C. Little difference was found in time to mass hatch at a given temperature among yellow perch (Hokanson and Kleiner 1974), Eurasian perch (Swift 1965; Kokurewicz 1969), pikeperch (Deelder and Willemsen 1964; Kokurewicz 1969; Muntyan 1975), and walleye and sauger (Smith and Koenst 1975), except that pikeperch developed at higher temperatures. Both perches and the pikeperch tended to hatch prematurely at low incubation temperatures where survival was low.

High temperatures can shorten the time for feeding opportunities of newly hatched larvae. The median period between swim-up and death of unfed yellow perch larvae was 9 days at 19.8°C and 21 days at 10.5°C (Hokanson and Kleiner 1974). Feeding trials at higher temperatures suggested that feeding started when the larvae became free-swimming. The critical period when survival-dependent feeding of larval perch must start is even shorter than the aforementioned intervals, since death of unfed larval fishes occurs when offered food after a certain degree of emaciation is reached (Toetz 1966). Woynarovich (1960) reported that pikeperch larvae were unable to withstand starvation for ½ day at the start of feeding, whereas larvae 8–10 days old could survive as long as 2 days without food. Studies by Priegel (1970) indicated that walleye larvae in the Wolf River, Wisconsin, starved to death unless they reached a lake environment where plankton production was high within 3–5 days after hatching. In larval perch that received no food during the first 7 days after hatching and were then allowed to feed for 20 days, mortality was 94% in aquaria and 66% in a pond (Menshutkin et al. 1968). All larvae starved for 9 days after hatching died when placed in the pond or aquaria. In summary, the importance of timing of larval development with production of specific food organisms is evident.

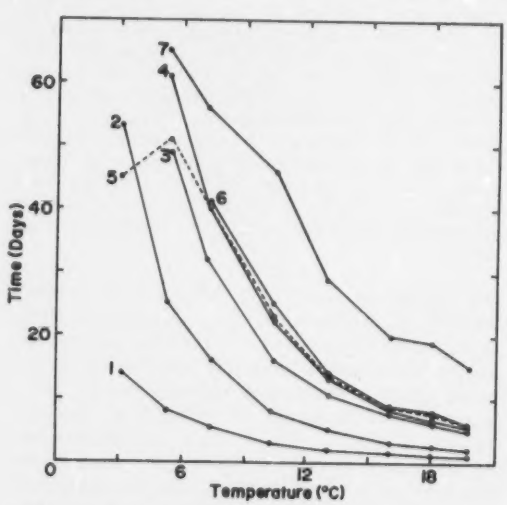

FIG. 5. Median times for development to various stages of yellow perch embryos and larvae at various temperatures. 1, Neural keel; 2, heart beat; 3, retinal pigmentation; 4, branchial respiration; 5, mass hatch; 6, swim-up larvae; 7, mortality of unfed larvae (from Hokanson and Kleiner 1974).

Year-class strength — Reproduction of *Perca* and *Stizostedion* spp. depends on a rising temperature regimen for optimal recruitment, given other favorable conditions. Busch et al. (1975) observed a high positive correlation between walleye year-class strength and rate and regularity of water-temperature rise on the spawning grounds during the spawning and incubation periods. Strong year-classes of perch (Kipling 1976) and pikeperch (Nagięć 1977) developed when the water is warm during periods of reproduction, though suitable temperatures do not always produce strong year-classes. Water temperature has not always been implicated as the sole factor influencing recruitment of percids. Willemsen (1977) and Clady (1976) concluded that a sequence of favorable factors probably determines the success of a year-class and that no one factor can be considered as a decisive cause for fluctuations in year-class strength.

Growth

Bioenergetics and growth — Growth can be viewed as the net effect of the environment on the relation between food consumption, metabolism, and activities of an organism. Warren (1971) discussed these theoretical relationships and the fate of consumed food in terms of a bioenergetic budget (Fig. 6). Temperature influences food-consumption rate of a fixed ration and distribution of assimilated energy into different

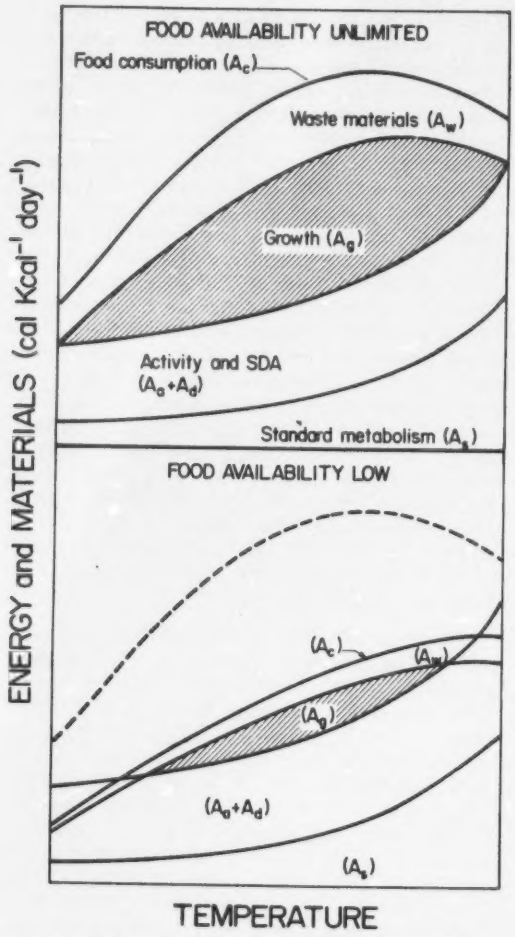

FIG. 6. Theoretical effects of temperature change on the food consumption, energy budget, and scope for growth of a hypothetical poikilothermic animal having food available in different amounts (from Warren 1971).

components such as metabolism, activity, and growth of the organism.

Several factors besides temperature should be taken into account when one compares growth studies conducted under different experimental conditions or analyzes population differences. The proportion of assimilated energy available for growth increases with temperature to a peak, and then declines as temperature increases further (Fig. 7). For small fish fed unlimited rations, the optimum temperature is skewed toward the upper biokinetic range, only a few degrees below the upper lethal temperature. Deviations from

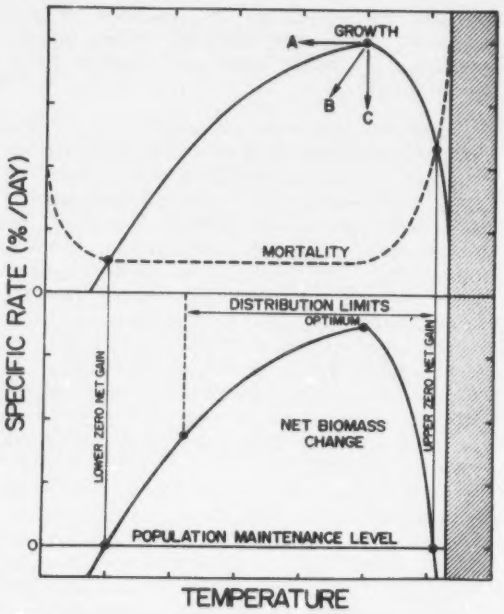

FIG. 7. Constant temperature effects on specific rates of growth (g), mortality (i), and net biomass change ($k = g - i$) for a hypothetical fish species fed excess rations. The zone of thermal resistance, where survival is time-dependent, is represented by the shaded area, bounded on the left margin by the ultimate upper incipient lethal temperature. Graphical endpoints that have particular physiological and ecological significance are identified by circles and labeled in the lower panel. Predicted shifts in growth response and optimum endpoints attributed to different stimuli illustrated in upper panel: A, diel fluctuation of acclimatization temperature of *Salmo gairdneri* (Hokanson et al. 1977); B, restricted food rations of *Oncorhynchus nerka* (Brett et al. 1969); C, increased initial size of *O. nerka* (Shelbourn et al. 1973).

this pattern of growth are influenced by several variables as illustrated in Fig. 7. Diel temperature fluctuations (A) shifted the growth response of *Salmo gairdneri* horizontally towards a lower mean equivalent constant temperature in direct proportion to the amplitude of the cycle (Hokanson et al. 1977). Temperature fluctuations enhance growth in relation to corresponding mean constant temperature levels below the optimum, and retard growth at higher temperatures. Restricted rations (B) can reduce the scope for growth and optimum temperatures of *Oncorhynchus nerka* (Brett et al. 1969). Increased size (C) can also decrease growth rate of *O. nerka* at all temperatures which produces a less pro-

TABLE 4. Some optimum temperatures for various percids.

Species	Growth optimum		Temp preference[a] (°C)		Physiological optimum (°C)
	Initial size or age	Temp (°C)			
Sauger	9.6 cm	22.0[c]	18.6–19.2 (lake)	(F)[b]	22.0
			22–28 (stream)	(F)[i]	
Walleye	8.5 cm	22.1[c]	20.6–23.2	(F)[b]	22.6
	6.5 cm	25.2[c]	21	(F)[j]	
Yellow perch	5.2–23.7 g (Fall–spring study)	23[d]	20.0–29.0	(L)[k,l,m]	24.7
			19.7–27.1	(F)[b,n]	
	0.5 g (Summer)	28[e]			
Eurasian perch	2 yr (15–16 cm)	26[f]	18–27.3	(F)[o,p]	25.4
	Larvae	25–30[g]			
Ruffe	Larvae	25–30[g]			
Pikeperch	1 yr	28–30[f]	29	(L)[f]	27.3
	13 cm		24	(F)[q]	

[a]Laboratory (L) final preferendum based usually on juvenile fish; field distribution values (F) usually based on adults.

[b]Average of reported growth optima and temperature preferences of a given species.

[c]Smith and Koenst (1975); [d]Schneider (1973); [e]McCormick (1976); [f]Willemsen, personal communication; [g]Kammerer (1907); [h]Ferguson (1958); [i]Gammon (1971); [j]Johnson (1969); [k]McCauley and Read (1973); [l]Barans and Tubb (1973); [m]McCauley (1977); [n]Neill and Magnuson (1974); [o]Neuman (1974); [p]Horoszewicz (1973); [q]Deelder and Willemsen (1964).

nounced optimum temperature (Shelbourn et al. 1973). Growth rates of young walleye and yellow perch were faster for 16-h days than for 8-h days at both 16 and 22°C (Huh et al. 1976). Growth of young walleye appeared to be temperature dependent, whereas that of yellow perch was more photoperiod dependent. Inadequate food type can also increase maintenance requirements and reduce growth rate of yellow perch at the higher temperatures (Schneider 1973).

Optimum growth temperatures for six percids ranged from 22 to 28°C (Table 4); they were lowest in walleye and sauger, intermediate in the two perches and the ruffe, and highest in the pikeperch. Variation in growth optima within species reflects differences in age, diet, and season of test. Large differences between treatment intervals also decrease the accuracy of the reported optimum value among tests. In contrast, the growth optima ranged from 15 to 18°C for three temperate stenotherms, from 26 to 27°C for two other temperate mesotherms, and from 30 to 32°C for four temperate eurytherms (Table 3).

Annual growth — Annual growth increments are a function of the size of fish and they accumulate daily increments of growth that vary with the available food supply and temperature over the year. Food supplies are known to vary seasonally and thus would tend to destroy any long-term correlation with temperature. Food-consumption rate of a walleye population in Lake of the Woods, Minnesota, was 1% of body weight during June, 2% during July, and 3% during August and September (Swenson and Smith 1973). Food consumption of adult perch in Loch Leven, Scotland, decreased from 6.5 and 6.7% of their body weights in June and July, respectively, to 3.2% in September (Thorpe 1974). Energy content of food items is also variable and may be seasonal (Kelso 1973). If one truly wants to understand how temperature influences annual growth, one must reexamine seasonal growth relationships of populations in the context of bioenergetics, which will require frequent monitoring of environmental conditions prevailing during the entire year.

Descriptions of annual increments of growth provide limited information of the effects of the environment on seasonal growth (Warren 1971). Low correlation between annual growth increments and mean water temperature does not imply that temperature has no effect, since temperature is known to exert a continuous influence on the food consumption and fate of assimilated energy. Low correlation may result from lack of accurate environmental information including fish-acclimatization temperature, prey and predator biomass, high population density (which restricts food rations), seasonal variations in food

supply, and use of inappropriate statistical models of growth due to lack of sound experimental data. Coble (1966) found a high correlation between annual growth increment of yellow perch and mean water temperature (14.5–16.0°C) from June to October in South Bay, Lake Huron. Such temperatures are considerably below the optimum or preferred temperatures of yellow perch, suggesting that temperature was controlling growth in this environment even when rations available to fish were restricted. LeCren (1958) found a high correlation between annual growth and degree-days above 14°C over a 22-yr period in an exploited population of Eurasian perch in Lake Windermere, England. Growth rate of this population improved in response to exploitation, suggesting that food was limiting growth in the unexploited population.

Survival

Lethal temperatures — The lethal temperatures of percids are variable because they provide the mechanism to resist temperature extremes during seasonal changes. Fry (1947) provided several useful definitions in measurement of the lethal factor. The lethal temperatures of fish have been determined by either the incipient lethal temperature or the critical thermal maximum (CTM) method. In tests in which temperature was increased 6°C/h, the CTM was about 3.5°C higher than the respective incipient lethal temperature (Horoszewicz 1973). The CTM method is commonly used by Eurasian authors, whereas the incipient lethal temperature test is commonly used by North American authors.

Any factor that influences thermal acclimation or the effective time influences the apparent lethal temperature. When an organism is transferred from one water temperature to another, thermal acclimation takes place within hours for increasing temperatures, but is not completed for several days for decreasing temperatures (Brett 1944). Fish acclimated to diel temperature fluctuations compensate for high and low temperatures simultaneously and have an increased range of temperature tolerance (Feldmeth et al. 1974). Pupfish, *Cyprinodon nevadensis amargosae*, acclimated to a diel temperature cycle from 15 to 35°C had critical thermal maxima equal to those acclimated to constant 35°C and had critical thermal minima equal to those acclimated to constant 25°C (the mean of the cycle). The critical thermal minimum, which reached its lowest point after 22 days of acclimation, was changed more slowly than the maximum, which was reached in <7 days. Hart (1952) observed seasonal differences in thermal tolerance of several species; however, some of these differences were due to incomplete acclimation in winter studies, which was attributed to inadequate acclimation time or inadequate feed in stock tanks. Seasonal changes in day length may contribute to these differences in thermal responsiveness (Fry 1957). Brett (1944) observed no effect of starvation for 40 days on the upper incipient lethal temperature of *Ameiurus nebulosus* in summer tests. Low dissolved oxygen concentrations can block thermal acclimation and normal seasonal response to temperature (Brett 1946).

Juveniles are perhaps the most thermally tolerant phase in the life cycle of percids. For example, the ultimate upper incipient lethal temperature of juvenile and adult yellow perch varied from 29.2 to more than 33° C for various test conditions (Table 5), but the 24-h TL50 for newly hatched larvae was 28° C, as previously described. Other examples are sparse among percids, but examples are listed for cohabitant species in Table 3. Weatherley (1963b) and Horoszewicz (1973) concluded that size did not influence lethal temperatures among juvenile fish; however, Bailey (1955) observed that adults died and only juveniles survived high temperatures in a Michigan pond.

In juvenile percids, the ultimate upper incipient lethal temperatures generally fell in the range between 29.2 and 35.0°C for various species and test conditions (Table 5). Since tests were seldom conducted under closely similar conditions, the conditions for acclimation (laboratory) or acclimatization (field), age, season, and test duration or rate of temperature rise are reported so that the experimental variation may be noted. Thermal tolerance appears to be lowest in the walleye and sauger, and highest in pikeperch. The upper incipient lethal temperature of yellow perch alone varied from 29.2 to more than 33°C, depending on test conditions. The highest values of the ultimate upper incipient lethal temperature occurred for summer tests at the highest acclimation temperatures, increasing slowly to test temperatures. Under comparable conditions the two perches had almost identical thermal tolerance limits. The ruffe had a relatively low upper incipient lethal temperature of 30.4°C; however, the acclimation temperature (20°C) was the lowest in this series. The critical thermal maximum for ruffe was similar to that for both perches considering differences in acclimation and rate of temperature increase. In contrast, the ultimate upper incipient lethal temperature of juvenile cohabitants ranged from 25.0 to 26.5°C for three temperate stenotherms, from 29 to 33°C for two other temperate mesotherms, and from 34 to 37°C for four temperate eurytherms (Table 3).

TABLE 5. Lethal temperatures for various percids.

Species	Acclimation temp (°C)	Life stage[a]	Season[b]	Ultimate upper incipient lethal temp[c] (°C)	Critical thermal max[d] (°C)
Walleye	25.8 (2 wk) 3–4°C/h to test temp	J — 11.5 cm	F	31.6[e] (96)	
Sauger	25.8 (2 wk)	J — 11.9 cm	F	30.4[e] (96)	
Yellow perch	23–25 (field)	A — 12.5 cm	Su	30.9[f] (12)	
	22–24 (field)	J, A — 2.9 to 50 g	Su	29.2[g] (24)	
	25 (4 days)		Su	32.3[h] (13)	
	25 (20 days)	J — 6 to 24 g	W	29.7[i] (83)	33.4[i] (1)
	28 (1°C/day to test temp)	J — 0.5 g	Su	33–34[j] (24)	
Eurasian perch	25 (24 days)	J — 8.4 cm	S	31.4[k] (16.7)	
	30 (0.5°C/day)	J — (2 yr)		33.5[l] (24)	
	27.3 (field)	J	Su	32[m] (< 100)	35.9[m] (6)
	30 (7 days)	J — 0.9 to 2.2 g	Su		35.5[n] (4)
Ruffe	20 (11 days)	J — 8.6 cm	F	30.4[k] (16.7)	
	24.1–25.7 (field)	J — 2.8 to 6.2 cm	Su		34.5[m] (6.0 to 7.2)
Pikeperch	25.6 (field)	J — 3.6 to 9.3 cm	Su	34.3[m] (16.7)	37.0[m] (6.0 to 7.2)
	30 (0.5°C/day to test temp)	J — (1 yr)	W	35.0[l] (24)	

[a]A, adult; J, juvenile; total length in centimetres; wet weight in grams.
[b]F, fall; W, winter; S, spring; Su, summer.
[c]Effective time in hours in parentheses. Fish exposed to sudden temperature increases except where noted.
[d]Rate of temperature increase (°C/h) in parentheses.
[e]Smith and Koenst (1975); [f]Brett (1944); [g]Black (1953); [h]Hart (1952); [i]Hart (1947); [j]McCormick (1976); [k]Alabaster and Downing (1966); [l]Willemsen, personal communication; [m]Horoszewicz (1973); [n]Weatherley (1963b).

The lethal temperatures were generally 6–10°C higher than the growth optima among cold-water species, but only 3–6°C higher than the growth optima among warm water species. Optimal performance near lethal temperatures allows a wider thermal range for activity and scope for growth among the warmwater species.

Annual survival — The effects of food, fish size, and temperature regimes are important to understanding seasonal mortality among fish populations. Several authors have reported increased mortality in growth experiments at supra-optimal temperatures below the incipient lethal level (Strawn 1961; Smith and Koenst 1975; Brett et al. 1969). Food can act as an accessory factor contributing to increased mortality among fish reared at elevated temperatures (Fig. 7). A 96-h TL50 corresponds with a specific mortality rate of 17.3%/day. In the biokinetic range for growth below the optimum temperature, specific mortality rate declined to a low constant rate <0.5%/day among larval and young fishes (Hokanson et al. 1973a; McCormick 1976;

Hokanson et al. 1977). Within these normal temperature ranges, other factors such as food (Dobie 1969; Alm 1954; Forney 1974) and cannibalism or predation (Alm 1951; Sumari 1971) can limit survival.

Low winter temperatures can also contribute to increased mortality in fish populations (Fig. 7). Juvenile and older percids are considered able to survive temperatures near freezing (Hart 1947), but exposure periods for lower incipient lethal temperature tests are usually <1 wk. Some evidence suggests that in northern habitats fish must reach a certain size to survive their first winter. Survival of percid larvae is poor below 10°C, as noted previously. Yearling walleye, like the young of other species, were rather sparse in Canada's northern waters (Regier et al. 1969). Forney (1966) observed that population mean lengths of young-of-the-year walleye from Oneida Lake, New York, increased between fall and the following spring and attributed the size increase to selective mortality among smaller fish rather than to growth during the winter. Svardson and Molin (1973) correlated year-class strength of pikeperch with summer temperatures; the higher summer temperatures promoted growth, and ultimately overwinter survival. A strong selective mortality of females occurred among stunted populations of yellow perch in some Laurentian lakes of Canada (Newsome and LeDuc 1975). The mature female, because of lack of food in summer, could not build sufficiently large fat reserves to maintain normal body and maturation functions throughout the winter. Bacterial infections and mortality in fish populations were most intense in the spring, as the water temperature increased, and were lowest in summer, when antibody production was high (Bisset 1948). Acquired antibody titer was reduced and antibody production was nil at winter temperatures.

Net biomass change — Knowledge of the seasonal course of fish growth and mortality helps explain the magnitude of biomass at a given time and may provide insight into factors affecting production and yield. The specific rate of net biomass change (k) is equal to the specific growth rate (g) minus the specific mortality rate (i) (after Ricker 1958); the relationship between these parameters is illustrated in Fig. 7. The "population maintenance level" is equivalent to the initial weight of the population or the weight over some time interval whenever the specific growth and mortality rates are equal. The graphic endpoints that intersect the population maintenance level describe the lower and upper zero net gain limits for those test conditions. These graphical endpoints provide additional reference points to correlate with distribution limits of a species. These statistics are not readily available in the literature because mortality frequently has not been reported in growth studies, or tests have been conducted over only a narrow temperature range. McCormick (1976) provided a complete description of specific growth and mortality rates over the biokinetic range of juvenile yellow perch fed excess rations. If the abnormal perch at 32°C are considered as deaths, then the lower and upper zero net biomass gain limits were 6 and 31°C, respectively, and the growth optimum for excess rations was 28°C. The upper zero net biomass gain for juvenile walleye was 29°C, as graphically extrapolated from the data of Smith and Koenst (1975). This model of population growth accounts for maximum rate of biomass increase at temperatures near optimum for a given food ration. Supraoptimal temperatures produce a small biomass consisting of a few large individuals, and suboptimal temperatures produce large numbers of smaller individuals (Hokanson et al. 1977). This model also accounts for reduction in population biomass and negative production at temperatures outside the limits of zero net biomass gain, as has been reported during the winter in natural populations (Chapman 1967; Kelso and Ward 1972).

Activity

Preferred temperature — Multiple directive stimuli influence fish activity and contribute towards large variations in preferred temperatures of percids. Fry (1947) provided several useful definitions of activity and preferred temperature relations among fishes. Observations of percids temperature preference in laboratory and field studies varied from 18 to 29°C (Table 4). The variation from 19.7 to 29.0°C in yellow perch alone obscures differences among species. Yellow perch are difficult to condition to the gradient tank and are imprecise in their thermal preference. McCauley and Read (1973) reported a mean final preferendum for yearling yellow perch in summer of 23.3°C with SD = ±2.5°C. This value indicates that 99% of the observations of temperature selection (i.e. mean ±3 SD) fell in a range from 15.8 to 30.8°C in their study. Yellow perch continue to invade temperatures in excess of their upper incipient lethal temperature and die, especially when acclimated to low temperatures (Ferguson 1958; Barans and Tubb 1973).

Acclimation temperature is a principal factor influencing temperature preference (Fry 1947). At low acclimation temperature fish have a strong tendency to move into warm water such as ther-

mal plumes or the epilimnion. At acclimation temperatures above the final preferendum, fish tend to seek cooler water refugia such as the hypolimnion or groundwater springs. Barans and Tubb (1973) reported that preferred temperatures of young yellow perch varied from 13 to 29°C when ambient Lake Erie temperatures varied from 1 to 24°C, respectively, and no final preferendum was measured.

Young fish generally selected higher temperatures than adults in all seasons. The high preferred temperature of 29°C observed for young-of-the-year yellow perch in summer by Barans and Tubb (1973) corresponds closely to the growth optimum (28°C) reported for similar-aged fish in another summer test (McCormick 1976). McCauley and Read (1973) observed that juvenile yellow perch selected temperatures 3°C higher than adults when acclimated to 24°C during fall. McCauley (1977) found no marked seasonal difference in temperature preference of adult yellow perch at a given acclimation temperature, but found that temperature preference in winter of yellow perch acclimated at 5°C was 13°C, and thus higher than the safe limit for maturation (<10°C). Acclimation of adults to constant temperatures for periods up to 1 yr affects gonad maturation and resorption and perhaps influences the normal thermal responsiveness of the species.

Studies on the relation of temperature to tolerance, preference, metabolic rate, performance, circulation, and growth all point to a common physiological optimum for a given species (Brett 1971). Therefore, growth optima and preferred temperatures were averaged to derive an estimate of the physiological optimum for a species. The physiological optima varied from 22°C for walleye and sauger, 25°C for Eurasian and yellow perch, to 27°C for pikeperch (Table 4). In contrast, the physiological optima varied from 15 to 18°C for three temperate stenotherms, from 26 to 27°C for two other temperate mesotherms, and from 30 to 32°C for four temperate eurytherms (Table 3).

Field distribution — Catch per unit effort of a species along a habitat gradient, expressed as a range or median temperature, provides useful information on a species' field distribution. Dendy (1948) concluded that accurate predictions of fish-depth distribution could be made on the basis of the thermal profile of a stratified waterbody if allowance was made for unfavorable oxygen concentrations. He found sauger at a greater depth and lower temperature stratum (18.6–19.2°C) than walleye (20.6–23.2°C) in Tennessee reservoirs. Swenson and Smith (1976) made similar observations in Lake of the Woods, Minnesota. Laboratory and field temperature preferences of *Perca* spp. covered a similar intermediate range (18–29°C) among percids (Table 4). Pikeperch apparently have the highest preferred temperatures (24–29°C) among percids. The range of values for field distribution reported in Table 4 reflects a restricted distribution where higher or lower temperatures were available in their respective habitats. Stream populations may have higher field-distribution limits because depth or light are not covariates with temperature along a horizontal gradient. Hile and Juday (1941) recognized that the bathymetric distribution of certain species and age-groups was not always correlated with temperature and oxygen in various lakes and that local conditions go far towards obscuring their influence. Therefore, a more critical evaluation of other directive factors that influence diel and seasonal migrations of percids follows.

Day length and light intensity can influence the diel activity cycle and acclimatization temperature of a fish. Walleye (Carlander and Cleary 1949; Niemuth et al. 1972), sauger (Nelson 1968), and pikeperch (Deelder and Willemsen 1964) are reported to have nocturnal behavior patterns and thrive in turbid waters, whereas ruffe (Kammerer 1907), yellow perch (Hasler and Bardach 1949; Scott 1955), and the Eurasian perch (Eriksson 1974) are diurnal species. Larval yellow perch were most abundant in surface waters at night, whereas older fish were inactive, resting on the bottom (Ward and Robinson 1974). Yellow perch spawned at night in shallow water (Scott and Crossman 1973). Adult sauger had a nocturnal activity cycle in a shallow experimental stream channel with a horizontal temperature gradient (Fig. 8). The sauger were active in the warmwater zone at night, and rested in the open cool-water zone by day. Sauger A experienced a daily mean temperature of 10.4°C (range 7.0–13.0°C) and traveled 1097 m, while sauger B experienced a daily mean temperature of 6.8°C (range 5.3–11.4°C) and traveled 2804 m. In the absence of a heated gradient when the channels were covered by ice and snow, sauger were diurnal. Daytime activity of walleye and sauger in shallow water was increased by approach of a storm, low light intensity, wind action on shallow reefs, and turbid water (Eschmeyer 1950; Arnold 1960; Scott and Crossman 1973; Scherer 1976). Sauger generally thrive in a more turbid water habitat than walleye (Scott and Crossman 1973), which may account for a deeper bathymetric distribution of sauger in the same habitat.

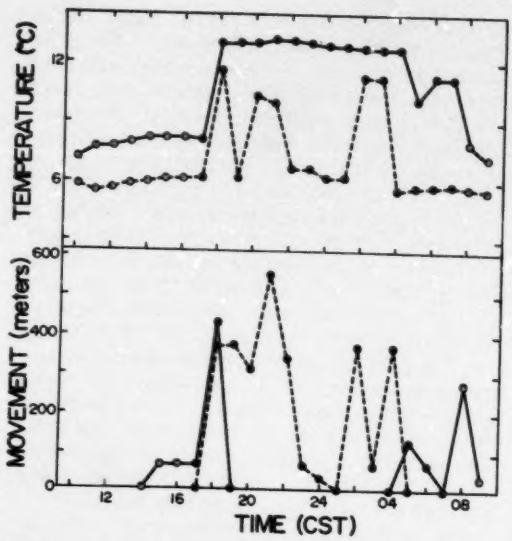

FIG. 8. Diel movements and acclimatization temperatures of two adult sauger (*S. canadense*) in a thermal gradient (5.3–13.4°C) in an outdoor experimental stream channel (518 m long) on January 6–7, 1975, as determined from tagging with ultrasonic transmitters. ———, sauger A; – – – – – –, sauger B; ○, daylight; ●, darkness (Environmental Research Laboratory–Duluth, unpublished data).

Food distribution and abundance can act as directive factors influencing fish distribution and activity. Swenson and Smith (1973) observed that walleye feeding in summer was uniformly distributed throughout the day and night during periods of low food consumption. When food consumption increased, feeding activity was greater at night and during early morning hours. In Lac la Ronge, Saskatchewan, walleye followed their cold-water prey, *Coregonus artedii*, offshore into deeper water in summer, even though the open waters were cooler than their temperature preference (Rawson 1957). In midlatitude waters walleye fed on prey such as yellow perch and benthic invertebrates found within their preferred temperature range (Dobie 1966). *Coregonus artedii* were not used as food in these waters except in cooler seasons when they were near shore. In a southern California reservoir walleye fed almost exclusively on warmwater prey such as *Dorosoma petenense* and were found in the warm surface waters at night (Miller 1967). Diel movements of pikeperch larvae corresponded closely to those of their prey (Kudrinskaya 1970a). Larvae followed copepods out to the warmer river channel, where larval concentration increased 40-fold in surface waters at night and only 4-fold in bottom layers; in contrast, the larvae were 15–20 times more abundant in bottom than in upper layers during daylight. Food availability increases the proportion of time fish spend at a nonpreferred temperature (Neill and Magnuson 1974). Inferences of thermal history or acclimatization temperature based on catch data from one portion of a day may be of relatively little value.

Age also plays an important role in the seasonal migration and temperature history of fish stocks. Ferguson (1958) noted that final preferenda of young fish in laboratory tests were higher than thermal limits for distribution of adults in field observations. Hile and Juday (1941) described an exception to this depth distribution, whereby small yellow perch were found at greater depths than larger ones. Tagging studies of walleye stocks suggested that the shallow, western basin of Lake Erie was a milling or mixing area for juveniles, whereas southern Lake Huron and the north shore of central and eastern Lake Erie were occupied mainly by adults (Ferguson and Derksen 1971). All percid larvae have a pelagic existence in offshore areas and migrate to the littoral area by late summer (Faber 1967; Priegel 1969; Kudrinskaya 1970a; Kuznetsov 1970; Spykerman 1974; Ward and Robinson 1974). The shoreward migrations of young percids are coincident with changes in food preferences from zooplankton to littoral forms such as benthic invertebrates and fish.

The maturation cycle and physiological condition of adult percids is important in governing seasonal migrations of fish stocks. The Eurasian perch showed a well-marked seasonal migration in Lake Windermere, England, living in the top 10 m in summer and at depths between 18 and 27 m in winter (Allen 1935). Perch migrate to the deeper waters in October and November and towards shore in April, when lake temperatures normally rise. This migration to deeper water in fall is coincident with gonadal development, as discussed previously. Allen argued that shoreward migrations are related to ripening of gonads since spawning takes place shortly thereafter. Furthermore, temperatures at the greater depths at which perch spend the winter do not increase much even by summer, whereas surface water temperatures increase to temperatures preferred for spawning. Similar seasonal migrations have been observed in yellow perch (Ferguson 1958; Brazo 1973) and walleye (Forney 1966; Johnson 1969). This seasonal migration of adult percids to deeper water in fall and winter and shoreward in the spring has not been described by laboratory studies of preferred temperatures.

Multiple stimuli may direct percids offshore by fall to bring them into conditions favorable for gonad maturation. Offshore migrations begin in

summer as surface water temperatures increase and the thermocline depth increases. Percids seek the deeper waters which remain warmer than the shoals in late fall and early winter. Eriksson (1974) observed the diel and annual rhythm of activity and vertical distribution of Eurasian perch in a large laboratory tank. During winter perch were less active and stayed near the bottom of the tank. During summer they were about as numerous in the upper part of the tank as in the lower. Thermal plumes to the upper Mississippi River did not attract yellow perch in winter, but spawning aggregations frequented the area in spring (M. J. Ross, University of Minnesota, Minneapolis, Minn., personal communication). Neill and Magnuson (1974) also observed that yellow perch were less abundant in thermal plumes in all seasons than in unheated areas. Possibly a preference for low light intensity or ice cover in winter reinforces the low temperature requirements for gonad maturation and guides the fish away from the influence of onshore thermal plumes.

Temperature gradients on the spawning grounds may be a directive factor in spawning migrations of percids. Optimal temperatures for spawning and gamete viability are considerably higher than those required for maturation. Once maturation is completed, spawning migrations may be directed towards optimal spawning temperatures. In higher latitudes walleye spawning runs began while ice remained on the main lake systems. The influx of warmer water from tributary systems was a stimulus to upstream spawning migrations (Rawson 1957; Priegel 1970). In years when the water in the Gulf of Riga, Latvia, warmed up slowly, the Eurasian perch abandoned its ordinary spawning site over algae-covered stony shallows and spawned over shallow sandy banks where water temperatures were 5–8°C higher (Berzins 1949). Walleye spawning runs from Oneida Lake, New York, into Scriba Creek were blocked when creek temperatures were lower than lake temperatures (Forney 1967). Similar examples have been observed whereby spawning grounds of pikeperch have shifted with temperature changes (Bastl 1969; Biliy 1963). Significance of thermal gradients in the vicinity of spawning grounds needs to be more critically evaluated in relation to optimal temperatures for gamete viability.

Adaptations to the Seasonal Temperature Cycle

The temperature history of fish populations must be accurately described before the role of temperature in the autecology of a given species can be adequately described. A historical compendium of freshwater fisheries and water-temperature data in the continental United States was recently compiled to supplement knowledge of temperature regimes where various species were found (Hokanson and Biesinger 1977). Stations with matched fish–temperature data sets were selected only from streams, since temperature data from well-mixed water bodies would be more representative of fish-population temperature experience than data from thermally stratified waters. The most complete field and laboratory data base existed for *Perca* spp. Therefore, correlations of physiological responses and endpoints to distribution limits for this genus serves as an example for percids that have similar physiological requirements. Once ecological relationships are established, one hopes that the collection of meaningful data for other species, and useful interpretations of the existing data, will be stimulated. The seasonal temperature envelope that describes the temperature limits for adaptation of yellow perch within the United States is shown in Fig. 9. The existing field data were compiled from 35 stations in the southern part of the native range of this species. Yellow perch are found as far north as Great Slave Lake at 63° N lat., across Alberta, James Bay, Quebec, New Brunswick, and Nova Scotia (Scott and Crossman 1973). The stations sampled were primarily from the upper Mississippi River drainage and Atlantic coastal streams from Maine to North Carolina.

Temperature requirements of *Perca* spp. are superimposed on the temperature regimes where both perches were present for comparison (Fig. 9). The evaluation of temperature limits to distribution of a species cannot be based only on presence data from the species' geographical range, but must be based on formal evaluative techniques that include knowledge of life-cycle requirements and experimental introductions beyond their indigenous range (Weatherley 1977). Therefore, it is necessary to seek information on extreme temperature limits where self-sustaining populations are known to survive when introduced beyond their natural range. The warmwater regimen is from the Darling River at Bourke, which represents the lowest latitudinal limits of distribution of introduced populations of *P. fluviatilus* in Australia. The coldwater regimen is from Big Trout Lake, which is the highest latitudinal limit of distribution of *P. flavescens* in Ontario.

Requirements for reproduction and bioenergetics of a species pose ultimate limits to distribution and abundance. Seasonal fluctuations in temperature are required in percid habitat to insure that requirements for growth and repro-

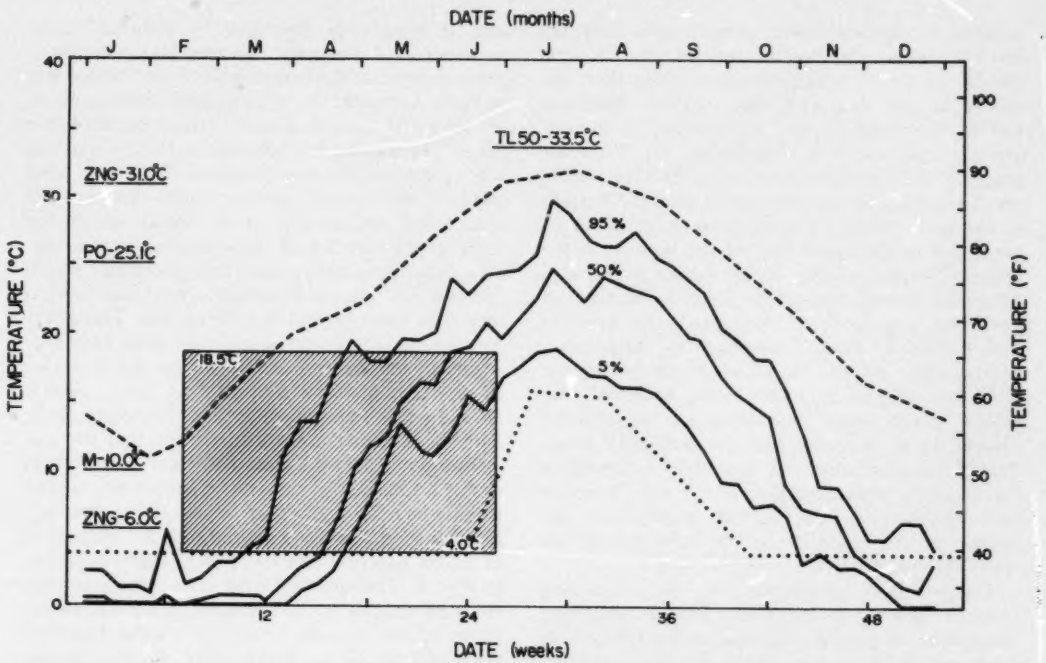

FIG. 9. Seasonal temperature envelope described by percentage occurrences (≤) of weekly mean temperatures where yellow perch were present in 35 stream stations throughout the United States. Temperature requirements of yellow perch for physiological optimum (PO), lower and upper zero net biomass gains (ZNG), ultimate upper incipient lethal temperature (TL50), maturation (M), and spawning (shaded area) are noted for comparison (from Hokanson and Biesinger 1977). Multiple endpoints for field and laboratory observations were averaged before plotting. – – – – –, water temperature in the Darling River at Bourke, Australia, just beyond the lower latitudinal limits of distribution of *P. fluviatilus* (from Weatherley 1963a); . . . . . , mean monthly epilimnetic temperatures of Big Trout Lake, Ontario, from 1959 to 1964, at the higher latitudinal limits of distribution of *P. flavescens* (R. A. Ryder, Min. Nat. Resour., Thunder Bay, Ont., personal communication).

duction are met. The increasing temperature requirements of successive early life phases show how percids adapt to the spring spawning period. Spawning and gamete viability is possible from about 4.0 to 18.5°C (Fig. 9). Shifts in spawning time among perch populations are related, in part, to availability of suitable spawning temperatures for different regimes in each locality. Perch inhabiting thermal regimens corresponding to the upper envelope (95 percentile) would be expected to spawn from mid-March to mid-May. Perch inhabiting regimens corresponding to the lower envelope (5 percentile) would be expected to spawn from early May to the end of June.

There are several types of adaptation in seasonal oogenesis among percids (Koshelev 1963). In adult percids with synchronous oocyte growth and isochronous spawning (e.g. *Perca* and *Stizostedion* spp.), environmental conditions have only limited effects on the duration of the stages of gonad maturity. As a consequence, there is only a shift in the spawning temperatures and change in spawning time by only a few weeks within stocks, sometimes at the expense of gamete viability. The spawning season of perch living in a cooling pond in Poland was advanced only slightly — spawning merely proceeded at higher temperatures (12–18°C) than elsewhere (EIFAC 1968). In Lac la Ronge, Saskatchewan, walleye spawning runs began at higher temperatures (7.2–11.1°C) in years when spawning occurred early (April 30–May 7) and at lower temperatures (3.3–7.2°C) in years when spawning was delayed by cold weather (May 17–21) (Rawson 1957). In the Lake Winnebago system, Wisconsin, the walleye spawning run started sooner in the warmer tributary river marshes (2.2–15.6°C) than in the larger, colder main lake (4–11.1°C) (Priegel 1970). Greater differences in spawning time observed among stocks living at tempera-

ture extremes may be due to longer term adaptations that influence time of first maturity which also determine the start of the annual endogenous reproductive rhythm and subsequent spawning periods in each respective habitat (Hokanson and Biesinger 1977).

Pikeperch are more adaptable to changing environmental conditions than are the two perches and walleye, since their oocyte growth periods (stages III–IV) are more asynchronous (Koshelev 1963). Pikeperch in Lake Glubokoe near Moscow, USSR, accumulated nutrients in the oocytes during fall and winter. In the south these periods of oocyte growth shifted to the spring. In some reservoirs female pikeperch omitted the period of resorption and limited ova growth (stage II of maturity), an omission that is more typical of species with batch spawning. Golovanenko et al. (1970) noted asynchronous maturation of the gonads of pikeperch in different size groups. Fish of medium size matured first during the spring spawning migration. A period of supplementary feeding was needed by smaller and larger females because of the higher energy requirements associated with metabolism and high fecundity, respectively. A protracted late spring produced more synchrony in the maturation of fish used in fish culture. Bastl (1969) suggested that the pikeperch adaptation to low spawning temperature in Orava Reservoir, Czechoslovakia, could be attributed to the rich forage supply.

The reproductive cycle of ruffe is most adaptable to changing environmental conditions. The rapid and asynchronous oocyte growth and lack of a resting stage II of maturity in ruffe lead to batch spawning and longer spawning periods than in *Perca* and *Stizostedion* spp. An extended spawning period has survival value for a species by assuring that all ova do not have the same temperature history and increasing the probability that some are deposited under favorable conditions for survival.

The maturation limit (10°C) for *Perca* spp. is approached by the winter minimum temperature in Australia (Fig. 9). This temperature regime appears to be above the limits for normal maturation. The Australian population spawned only in late August, which corresponds to late February in the northern hemisphere, at temperatures above 11.5°C (Weatherley 1963a). Lake (1967a) suggested that the possible damage of oocytes by high minimum temperatures preceding spawning may be another mechanism limiting perch distribution in Australia. The effects of the longer growing season, migrations, feeding regime, and seasonal and diel temperature fluctuations on gamete maturation of stocks living at lower latitudes need to be critically evaluated. Temperatures were within acceptable levels for maturation at all U.S. stream stations and were below 10°C for 21 wk at the upper envelope (95%).

The length of the growing season may limit the northward distribution of a species through retardations of maturation of adults and growth of young. Ryder et al. (1964) showed that the natural range of yellow perch extended northward in North America to a boundary corresponding to the 16°C isotherm for mean July air temperature. The mean water temperature in Big Trout Lake, Ontario, approached this minimum isotherm (Fig. 9). The time that temperatures exceed the lower zero net biomass gain value (6°C) determines the potential length of the growing season, depending upon food availability. The Ontario population would be expected to spawn in late June and early July immediately after ice break-up. The maximum length of the growing season of yellow perch was only 15 wk. The growing season of young-of-the-year would be even shorter. The threshold for larval survival (10°C) is exceeded for only 10 wk and low winter temperatures may limit survival of smaller individuals directly, or indirectly (through predation over an extended period of no growth). Low summer temperatures may also limit reproduction through inhibition of normal resorption processes in the ovary and proliferation of the new generation of oocytes. The lower envelope (5%) exceeded the lower zero net biomass gain value for 26 wk, and maximum growth potential during the peak of the growing season was only 38% of optimum. A maximum growth potential of at least 50% in midsummer was required for a wide variety of freshwater fishes (Hokanson and Biesinger 1977). This value is represented as the generalized lower limit to fish distribution in summer in Fig. 7.

The upper zero net biomass gain temperature (31°C) may be considered an upper limit to distribution of *Perca* spp. (Fig. 7 and 9). Weatherley (1963a) showed that the natural range of yellow perch extended southward in North America to a boundary corresponding to the 31°C isotherm for mean maximum midsummer air temperature and that introduced populations of Eurasian perch in Australia were limited by the same isotherm. The Australian population had a potentially continuous growing season, except in midsummer when the temperature exceeded the upper limit of zero net biomass gain for perch populations and reduction of biomass was possible. A potential growing season of 36 wk was likely for perch populations living at

temperatures approaching the upper envelope (95%). The maximum value in the upper envelope was 2–3°C above the physiological optimum for this species and it was about 3°C below the upper zero net biomass gain value for the same test. The median envelope approached the physiological optimum for this species only during the peak of the growing season. Maximum growth is not attainable throughout most of the year and growth potential can vary widely in different seasons throughout the geographical range where a species is present, depending upon temperatures in each habitat.

The lethal temperature of species provides a short-term survival mechanism to resist extreme fluctuations in environmental temperature. The ultimate upper incipient lethal temperature (33.5°C) was about 6°C above the upper envelope (95%) where yellow perch were present in the United States and 2°C above the Australian regimen (Fig. 9). Only the maximum temperature values listed in the data base by Hokanson and Biesinger (1977) approached the ultimate upper incipient lethal temperature for several fish species. In this compendium, the daily maximum temperature at the warmest station where sauger were present frequently exceeded their upper lethal temperature; the daily minimum never exceeded it. Eurasian perch were seen dying in the lower Lachlan River, Australia, during a heat wave when surface waters reached 33.3°C (Lake 1967b). Temperatures limiting distribution are always less than the upper incipient lethal temperature. Fish kills from heat are rare in nature and generally occur only when escapement is blocked or when the coolest water available to fish exceeds the lethal temperature or is deficient in oxygen.

Brett (1956) questioned whether lethality ever acted directly in influencing fish distribution and suggested that some other property or attribute correlated with the upper lethal temperature must be operating as a factor limiting fish distribution. Evidence to support his statement comes from observations that lethal temperatures are several degrees Celsius above natural distribution temperatures and that species with similar ultimate upper incipient lethal temperatures have different thermal limits of distribution in their natural habitat. Hokanson and Biesinger (1977) found a high positive correlation between the ultimate upper incipient lethal temperature and the physiological optimum and upper spawning threshold for eight fish species. If the lethal temperatures of species are correlated with ecological succession along a habitat gradient, ecological succession is also correlated with the species' basic requirements for reproduction and growth.

Thermoregulatory behavior is the mechanism by which fish stocks control their acclimatization temperature and optimize their physiological performance along a finite temperature gradient of each habitat. Close correspondence between distribution limits and temperature requirements for growth and reproduction of a species emphasizes the role of activity. The summer isotherms limiting distribution of *Perca* spp. (16–31°C) correspond closely to the range of preferred temperatures (Table 4) and distribution range in horizontal gradient tanks (McCauley and Read 1973). Multiple directive stimuli account for these distribution limits within and between waters. The temperature range selected by perch in their natural habitat is such that positive net biomass gain will occur, insuring a sustained yield of the species. Acclimatization temperatures of all self-sustaining perch populations probably fall within these isothermal limits, even though temperature characteristics of part of their habitat may fall outside this range. Finite temperatures available to fish in a given locality provide a wide range of behavioral adaptations in waters of different temperature characteristics.

Fish adapt to different temperature characteristics by changes in their diel activity cycle and seasonal migrations. Fish adjust to the summer maximum temperature through their diel activity cycles and avoidance or preference responses. Resultant temperature fluctuations are known to be beneficial to fish populations. Benefits of diel temperature fluctuations at mean temperatures below the physiological optimum include faster growth rates and expanded scope of thermal tolerance, compared to mean constant acclimation temperatures. Brett (1971) interpreted the diel vertical migration of *Oncorhynchus nerka* as a mechanism of behavioral thermoregulation that balances daily metabolic expenditures to conserve energy when food is limited. Likewise, seasonal changes in temperature are necessary to meet the changing requirements for reproduction and growth. Seasonal migrations of percids ensure that these changing requirements in their life cycle are met. Migrations may serve to guide a population to favorable spawning temperatures, but deposited ova are subjected to uncontrolled fluctuations of nature that can determine year-class strength.

Management Implications

Management of percid communities in different latitudes must be based on knowledge of how environmental and biotic factors regulate population structure, distribution, and abundance. Species are distributed over a wide range of

temperature conditions, and possibilities for population adaptation are immense. The adaptive capabilities of fish populations have been described by Beverton and Holt (1959). Data from 69 species of fish indicated a direct relationship between growth rate and mortality rate and maximum age and asymptotic length, and inverse correlations between maximum age and mortality rate and asymptotic length and growth rate. Comparisons with environmental data indicate that growth rate is affected by temperature and that asymptotic length is affected by food and temperature. Comparisons of the ratio of length at maturity to asymptotic length with maximum age suggest high ratios related to short life span. Reproductive drain is evident with fast growth and early maturity. Tanasiychuk (1974) and Colby et al. (1977) also observed a relation between fast growth rates, early maturity, and short life span in pikeperch and walleye. Southern populations are typified, relative to northern stocks, by accelerated growth and higher fecundity.

The background data for percids presented herein provides the basis for formulation of a hypothesis concerning stock variability in response to environmental temperature. It is acknowledged that local biotic and abiotic variables can mask any correlations with temperature within any given waterbody. Therefore, maximum expression of the temperature factor can be observed at geographical extremities of a species range. All variables that influence percid population dynamics and structure are assumed to be constant or not limiting, so that the controlling influence of temperature can be compared. The three acclimatization temperatures illustrated in Fig. 9 are the driving variables for the following predictions:

1) Coldwater regimen (lower envelope). This population is characterized by low rate of recruitment attributed to poor survival of larvae in summer and of the young over winter. Growth is slow and confined to summer. Age of maturity is high. Natural mortality of older age-groups is low; consequently populations consist of multiple age-groups and longevity is highest. Population may be distributed in surface waters throughout summer. Population biomass may be high in virgin stocks, but population resiliency is low.

2) Median envelope. This population has a variable rate of recruitment, depending on rate of temperature increase throughout the spawning season and food available for larvae. Growth rate is intermediate and limited to the postspawning period through early fall. Age of maturity, longevity, and number of age-groups are intermediate. Population is in surface waters in spring and early summer with gradual migration to deeper waters, older age-groups migrating first. Population biomass and resiliency is highest.

3) Warmwater regimen (Australian regimen and upper envelope). Recruitment is low and limited by proportion of females that mature and spawn and by high spawning temperatures that reduce gamete viability. Survival of larvae and young is limited by food supply and predation. Growth rate is high with a prolonged growing season from spring to fall, except for the warmest period in summer. Age of maturity is low. Natural mortality rate is high among all age-groups. This population is composed of a few age-groups and longevity is least. Percid distribution in summer is restricted to cold-water refugia such as the thermocline or hypoclimnion, which are less productive zones and occupy a smaller area of the waterbody. These stocks are most vulnerable to cultural eutrophication and exploitation. Population biomass is lowest.

These predictions emphasize the long-term and continuous influence of temperature history on percid population dynamics and structure. It is recognized that local factors, such as community relationships and morphoedaphic factors, can mask these trends. These temperature regimens would be expected to exert a different influence on species with requirements unlike those of percids. Population density and competition would exert their influence through limitations on food availability. Predation can be viewed as the relative influence of temperature on the appetite and activity of the predator in respect to its influence on growth and activity of the prey. The role of temperature in shaping aquatic communities is implicated through its effect on the relative population dynamics of each respective species and on species interactions.

The hypothesis should be verified by several approaches before management strategies are formulated:

1) Describe population dynamic characteristics and limnological conditions at geographical extremities of a species' range.

2) Derive population dynamic models to describe how a fish crop develops as a function of time for different temperature regimens (Kitchell and Stewart 1977).

3) Document changes in population dynamics and community structure at different temperature regimens in experimental ponds or streams.

The implications for management based on these predictions are the following:

1) Mechanisms of population regulation are different for each temperature regimen. Temperature effects are multiple, instantaneous, and cumulative.

2) Population resilience to forces of exploitation and cultural eutrophication varies in cold- and warmwater regimens. Populations living at mid-range or median regimens would be expected to be most resilient to exploitation and environmental degradation.

3) Pollution and community interactions exert similar effects as temperature on populations, and proper interpretation of cause–effect relationships requires thorough knowledge of temperature requirements of each species.

4) Management regulations cannot be universally applied for a given species throughout its geographical range.

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